# H I L G A R D I A

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## THE BIOLOGY OF APANTELES MEDICAGINIS MUESEBECK (Hymenoptera: Braconidae)[1]


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THE GENUS *Apanteles* is characterized biologically by being endoparasitic on various Lepidoptera. Numerous other orders have been reported as hosts, but in all cases where extensive studies have been carried out the non-lepidopterous records have proved to be erroneous. Some species of *Apanteles* are solitary and others are gregarious with a great variation in the arrangement of the cocoons. Some cocoons are constructed upon the host body and others are found apart from the host. Certain of the gregarious forms are disposed in a definitely arranged pattern while others appear to be scattered at random (Clausen, 1940).

Systematically, the genus *Apanteles* is placed in the superfamily Ichneumonidea, family Braconidae, and the subfamily Microgasterinae. Muesebeck (1921) characterized the genus in the following manner:

> Head usually transverse, rarely rostriform; occiput immargined; antennae slender, 18-segmented; eyes strongly hairy; thorax stout, broad; mesoscutum without parapsidal furrows, very rarely with the furrows evident posteriorly; propodeum usually more or less roughened, with or without a median longitudinal carina, sometimes incompletely areolated; anterior wing with the marginal cell open, only the first abscissa of the radius being present; second transverse cubitus entirely wanting, so that the second cubital cell is open behind; legs normal; abdomen sessile, varying in form from broad and depressed to very slender and strongly compressed; the two basal abdominal tergites usually more or less sculptured, ovipositor sheaths varying in length from subexserted to longer than the abdomen.

The genus *Apanteles* is readily separated from its nearest allies, *Microgaster* and *Microplitis,* by the total absence of the second transverse cubital nervure in the forewing. The genus is large and homogeneous. The many species are morphologically similar and each is highly variable. Consequently biological data must often be relied upon to separate the species.

### Apanteles Species Reported from Colias

*Colias* is a large and homogeneous genus of butterflies occurring in many of the arctic and temperate parts of the world (Remington, 1954; Talbot, 1935). It is largely northern in its distribution with only 10 of the listed


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56 species occurring in the southern hemisphere. The larvae of most species feed on legumes while the others feed on *Salix* and *Vaccinium*. In several parts of the world the larvae of the legume-feeding species have been reported to be attacked by members of the genus *Apanteles*. The published records

TABLE 1

HOST RECORDS FOR SPECIES OF *APANTELES* RECORDED FROM LEGUME-FEEDING *COLIAS*

| Species | Distribution | Hosts* |
|---|---|---|
| *A. medicaginis* Muesebeck | Western U.S. | *Colias philodice eurytheme* Bdv. (Michelbacher and Smith, 1943; and others) |
| *A. flaviconchae* Riley | Eastern U.S. | *Pseudaletia unipuncta* (Haw.) (Riley, 1882, 1889; Gibson, 1915; Britton, 1915; Viereck, 1916; Muesebeck, 1921; Muesebeck, Krombien, and Townes, 1951)<br>*Colias philodice philodice* Godart (Muesebeck, 1921; Muesebeck, Krombien, and Townes, 1951; Gerould, 1921)<br>*Colias philodice eurytheme* Bdv. (Floyd, 1940)<br>*Anthocaris midea* (Hbn.) (Muesebeck, 1921; Muesebeck, Krombien, and Townes, 1951)<br>*Plathypena scabra* (F.) (Muesebeck, 1921; Muesebeck, Krombien, and Townes, 1951; Kretzchmar, 1948) |
| *A. cassianus* Riley | Illinois; Colorado; Iowa | *Eurema nicippe* (Cramer) (Riley, 1889; Muesebeck, 1921; Muesebeck, Krombien, and Townes, 1951; Wolcott, 1927)<br>*?Colias philodice eurytheme* Bdv. (Riley, 1889; Muesebeck, 1921; Muesebeck, Krombien, and Townes, 1951)<br>*Kricogonia castalia* Fabr. (Wolcott, 1927) |
| *A. laeviceps* Ashmead | General over U.S. and lower Canada; restricted to higher elevations | Noctuidae (many records, Muesebeck, 1921; Muesebeck, Krombien, and Townes, 1951)<br>*?Colias philodice eurytheme* Bdv. (Muesebeck, 1921) |
| *A. limenitidis* (Riley) | Connecticut; Missouri Massachusetts | *Anthocaris midea* (Hbn.) (Muesebeck, Krombien, and Townes, 1951)<br>*Basilarchia archippus* Cramer (Muesebeck, 1921)<br>*?Colias philodice eurytheme* Bdv. (Essig, 1926; and others) |
| *A. ayerzai* Brethes | Argentina | *?Colias lesbia* (Fabr.) (Brethes, 1920b)<br>*Tatochila autodice* (Hbn.) (Blanchard, 1935) |
| *A. lesbia* Blanchard | Argentina | *Colias lesbia* (Fabr.) (Blanchard, 1947; Freiberg, 1947) |
| *A. zygaenarum* Marshall | Japan and Europe | *Colias hyale* (Linn.) (Watanabe, 1932)<br>*Zygaena filipendulae* Linn. (Marshall, 1885) |

* Doubtful records are preceded by a question mark.

are summarized in table 1. Because of the confusion surrounding these records certain details are discussed below.

*Apanteles cassianus* Riley 1882 was reported by Riley (1882, 1889) on the pierids *Eurema nicippe* Cramer and *Colias philodice eurytheme* Boisd. This record of *Colias* as a host arose from a collection by David Bruce in Colorado which was sent to Riley. Since this species has been recorded on both *Eurema nicippe* and *Kricogonia castalia* Fabr. (Wolcott, 1927) it is possible that *Colias* is an incidental host. The lack of records indicates that *Colias* is not an important host of this parasite.

*Apanteles laeviceps* Ashmead 1890 is a common parasite of noctuids in the United States and Canada (Muesebeck, 1921; Muesebeck, Krombien, and Townes, 1951; Decker, 1930, 1935; Snow, 1925). Muesebeck (1921) recorded *Colias philodice eurytheme* as a host of this species based on a rearing by D. J. Caffrey in Maxwell, New Mexico. Since this is the only record of this host, the rearing may have been from a noctuid occurring in a *Colias* infested field. Muesebeck, Krombien, and Townes (1951) did not repeat this record.

*Apanteles limenitidis* (Riley) 1871 was recorded by Muesebeck (1921) to be a parasite of *Basilarchia archippus* Cramer and *Anthocaris midea* (Hbn.). Other records in the early literature report additional hosts but are probably based on misidentifications (Riley, 1871; Weed, 1888). Some writers such as Essig (1926) also listed *Colias* as a host of this parasite but accurate records seem to be lacking. It is evident that records of this parasite on *Colias* arose from Riley's description of *A. flaviconchae* as a form of *A. limenitidis.*

*Apanteles ayerzai* Brethes 1920*a* and *A. lesbia* Blanchard 1942 have been described from *Colias lesbia* (Fabr.) in Argentina. *Colias lesbia* is similar to *C. philodice eurytheme* of the southwestern United States in its orange color and in its economic damage to alfalfa. Brethes (1920*a*) described *A. ayerzai* from this host, and from his description it appears to be quite different from our two North American species. The first and second abdominal tergites in *A. ayerzai* are smooth whereas in *A. medicaginis* and *A. flaviconchae* they are distinctly rugose. Brethes (1920*b*) reiterated that *A. ayerzai* was a parasite of *Colias lesbia;* however, Blanchard (1947) stated that it was very doubtful that *A. ayerzai* was a parasite of *Colias.* His conclusions were based on the fact that numerous *Apanteles* from *Colias* were examined and none resembled *A. ayerzai.* In addition, he stated that *A. williamsii* Blanchard (1935), a parasite of *Tatochila autodice* (Hbn.) from the same type locality, was a synonym of *A. ayerzai.* He felt that the larvae of *Tatochila* were mistaken for *Colias* and that *A. ayerzai* was not a parasite of *Colias* at all. *A. lesbia,* on the other hand, he reported as a common parasite of *Colias lesbia* in Argentina (Blanchard 1942, 1947). From the description it can be seen that this species closely resembles *A. medicaginis* and *A. flaviconchae.* Only slight color variations are apparent between these three species. Mention was not made as to whether *A. lesbia* was gregarious or solitary, but the description most closely resembles *A. flaviconchae.* One difference is that *A. lesbia* has white cocoons whereas the two Nearctic species normally have yellow cocoons. Freiberg (1947) reported *A. lesbia* to be common but not abundant on *Colias lesbia.*

*Apanteles zygaenarum* Marshall 1885 was recorded by Watanabe (1932), in Japan, as a gregarious parasite of *Colias hyale* (Linn.), which is a yellow species occurring in relatively cool, damp areas of Europe and Asia, a habitat analogous with that of *C. philodice philodice. A. zygaenarum* is a European species frequently recorded from moths of the genus *Zygaena* (Wilkinson, 1945; Lyle, 1916) and questionably reported from the butterfly *Melitaea aurinia.* Aside from the Japanese record it has never been reported on *Colias* and there is some doubt that it is a parasite of *Colias. A. zygaenarum* was

described by Marshall (1885) from *Zygaena filipendulae* Linn. This description was such that *A. flaviconchae* could easily be misidentified as *A. zygaenarum,* and for this reason it is probable that the *Apanteles* attacking *Colias hyale* in Japan is a species closely related to *A. flaviconchae.* Wilkinson (1945) redescribed *A. zygaenarum* Marshall, pointing out several minor differences between it and *A. flaviconchae,* but it can readily be seen how these two could be confused. He cited the Japanese record but mentioned that he had not seen Watanabe's material.

*Apanteles flaviconchae* Riley 1882 and *Apanteles medicaginis* Muesebeck 1947 are both commonly encountered parasites of *Colias philodice* in North America. *Apanteles flaviconchae* was first described by Riley (1882) as a form of *A. limenitidis* Riley. This form was distinguished as gregarious with yellow cocoons as compared with the solitary *A. limenitidis* with dull whitish cocoons. The host was presumed to be *Pseudaletia unipuncta* (Haworth) because the cocoons were found in a field infested with it (Riley, 1889). Gibson (1915) and Treherne (1916) repeated Riley's earlier statement that *A. limenitidis* form *flaviconchae* was apparently a parasite of *Pseudaletia unipuncta.* Britton (1915) and Viereck (1916) duplicated the statement of Gibson but used the combination *A. flaviconchae.* Muesebeck (1921) and Muesebeck, Krombien, and Townes (1951) recorded *A. flaviconchae* on *Pseudaletia unipuncta, Colias philodice* Godart, *Anthocaris midea* (Hbn.) (as *A. genutia* Fabr.) and *Plathypena scabra* Fabr. The distribution was given as "Maine to Va., west to Minn. and Texas." Gerould (1921), working on the genetics of *Colias philodice philodice,* recorded *A. flaviconchae* as having white cocoons when reared from blue-green *Colias,* whereas they were yellow when reared from normal yellow-green caterpillars. Floyd (1940), working on the alfalfa caterpillar, reported *A. flaviconchae* as being common on *Colias philodice eurytheme.* These specimens were determined by Muesebeck, and since they were reared from fifth-instar *Colias* they undoubtedly were *A. flaviconchae.* Kretzchmar (1948), working on soybean insects, stated that *A. flaviconchae* is important in the natural control of *Plathypena scabra* in Minnesota. Van den Bosch, Dietrick, and Hagen (1954) reported that *A. flaviconchae* had been introduced into California in an attempt to control *Colias philodice eurytheme.*

Prior to the description of *Apanteles medicaginis* in 1947, this species was confused with *A. flaviconchae.* Nevertheless, many of the early records of *A. flaviconchae* in the western United States can now be ascribed to *A. medicaginis.* This is possible because of the difference in biology of these two parasites. *A. medicaginis* is a solitary parasite emerging from the third- and fourth-instar *Colias* larvae, whereas *A. flaviconchae* is a gregarious species emerging from the fifth instar.

Wildermuth (1914), in the first published record which can be assigned to *Apanteles medicaginis,* stated that L. P. Rockwood "reared a goodly number of a small hymenopteron, *Apanteles* (*Protopanteles*) *flavicombae* Riley" from *Colias* at Salt Lake City. Although Wildermuth indicated that they were gregarious, Rockwood[3] stated that the parasites mentioned above emerged from small *Colias* as solitary parasites, and were determined by

[3] Rockwood, L. P. Letter to Ray F. Smith, June 23, 1951.

Gahan as *A. flaviconchae*. The solitary habit of these parasites conclusively indicates that the species involved was *A. medicaginis*. Schlosberg,[4] on the basis of unpublished data of the U.S.D.A. Division of Cereal and Forage Crops at Sacramento, reported that Holinger in 1919 collected 100 or more parasite cocoons in an alfalfa field near Tracy, California. These cocoons, which had come from *Colias philodice eurytheme* larvae, produced both adult parasites and hyperparasites in the laboratory. The hyperparasites were identified by Gahan as *Catolaccus aeneoviridis* (Girault), but no mention was made of identification of the primary parasite. Both the abundance of this parasite and the hyperparasite reared indicate that *A. medicaginis* was the species involved. Two additional records in these unpublished data were on specimens collected by Wilson in 1931 while sweeping alfalfa, and identified by Muesebeck as *A. flaviconchae*. We can safely assume that all these specimens were *A. medicaginis*. Michelbacher and Smith (1943), who studied the population trends of *C. philodice eurytheme* and *A. medicaginis*, collected heavily parasitized larvae of *Colias* in 1938. Adult *Apanteles* reared from this collection were later identified by Muesebeck as atypical color variants of *A. flaviconchae*. Additional specimens sent to Muesebeck in 1945 by Ray F. Smith provided morphological evidence that this was a subspecies of *A. flaviconchae*. The eastern *A. flaviconchae* female has a dark hind femur, whereas in the western female the hind femur is light. From the work of Michelbacher and Smith (1943) on the biology of this parasite it became evident that the western form, unlike the eastern, is a solitary parasite and emerges from the third and early fourth instars, as mentioned earlier. Smith[5] pointed out these biological differences to Muesebeck, who subsequently described the western form as *A. medicaginis*.

## Apanteles Medicaginis and A. Flaviconchae

**Morphological Differences.** Muesebeck (1947) characterized the morphological differences between *Apanteles flaviconchae* and *A. medicaginis* as follows:

> The only structural differences I have discovered between this species and *flaviconchae* are quantitative and subtle. They are not easily defined. In *medicaginis* the upper third of the face has a more or less distinct, median, longitudinal, keel-like elevation, of which there is only a faint suggestion in *flaviconchae*. The malar space in *medicaginis* is slightly longer and the face a little narrower than in *flaviconchae*, the face at its narrowest point being narrower than the eye height. In *flaviconchae* the punctures on the posterior half of the mesoscutum are separate although close, whereas in *medicaginis* they tend to be confluent, especially along the lines of the notaulices. The polished lateral margins of the second tergite are usually complete in *flaviconchae* and are continued upon the basal part of the third tergite, whereas in *medicaginis* they are usually not complete and seem never to extend upon the third tergite. Although these two species are not always readily separated by these distinctions, the females may normally be recognized at a glance. In *flaviconchae* the posterior femora are black in both sexes, but in *medicaginis* those of the female are reddish-yellow or, at the most, blackish along the upper and lower edges.

Subsequent work on *Apanteles medicaginis* has shown that individuals reared at low temperatures are of considerably darker color. Individuals reared at 15°C were noticeably darker and others which were allowed to

[4] Schlosberg, M. Letter to Ray F. Smith, June 15, 1951.

[5] Smith, Ray F. Letter to C. F. W. Muesebeck, September 10, 1946.

pupate at even lower temperatures were very dark. Females under these conditions often had the hind femora dark, and thus were very similar to *A. flaviconchae*. In nature these darker individuals have been found to occur in early and late season and in cooler localities.

Because these two species are so difficult to distinguish, a study of their genitalia was undertaken. Male and female genitalia were removed from specimens, boiled in potassium hydroxide, and mounted in balsam. The male genitalia were of little help, for the variation within each species was greater than between the species. Differences in the female genitalia, on the other hand, made it possible to separate the two species very readily. In both species the middle of the ovipositor tapers abruptly, forming a slender, slightly tapered terminal portion. In *Apanteles medicaginis* this terminal portion is about one third or less the total length of the ovipositor, whereas in *A. flaviconchae* it is always considerably longer than one third of the total length. Measurement of 20 ovipositors for each species showed that in *A. medicaginis* the ovipositor averaged 467 microns in length and the terminal narrow tip 148 microns, whereas in *A. flaviconchae* the total length was 440 microns and the terminal portion 174 microns. Although the total length of the ovipositors overlapped for the two species, the proportionate length of the terminal tip to the total length always made it possible to separate the two species. In addition to the ovipositor, the apodemes of the last abdominal segment, although variable in shape, seem to have specific differences. The upper end of each apodeme seems to terminate in a much more angular shape in *A. flaviconchae* than in *A. medicaginis*.

**Distribution in North America.** From our present knowledge of the distribution of these two species it seems unlikely that at the present time they are geographically isolated. *Apanteles medicaginis,* which is widely distributed in California, has also been found at Yuma, Arizona; Minden, Nevada; Twin Falls, Idaho; and Salt Lake City, Utah. Specimens which were reared from *Colias philodice eurytheme* in Lawrence, Kansas, by R. E. Beer were typical *A. medicaginis,* showing that this species extends east of the Rocky Mountains. A single *Colias* larva from Tulancingo, Hildago, Mexico, collected by Ray F. Smith, was parasitized by an *Apanteles* sp.; although larval identification is impossible, the solitary nature of this parasite strongly suggests that it is *A. medicaginis* or a closely related species. *A. flaviconchae* has been recorded from Missouri, Connecticut, Massachusetts, Maine, Maryland, and West Virginia (Muesebeck, 1921). In addition, it has been reported by Floyd (1940) in Louisiana and by Kretzchmar (1948) in Minnesota.

**Hosts.** Since *Apanteles medicaginis* and *A. flaviconchae* are very closely related morphologically but very distinct biologically, a consideration of their hosts is of particular interest. The components of *Colias philodice,* with which we are concerned in relation to *Apanteles,* are the eastern yellow *philodice,* considered by most workers to extend west to the Sierra Nevada; the western orange *eurytheme,* which extends east to the Atlantic; and *eriphyle,* which occurs in the northwestern part of the United States.

Klots (1932) in his generic revision of the Pieridae considered *Colias eurytheme* Boisd. and *C. philodice* Godart to be separate species. It must be remembered, however, that he was primarily interested in the generic level.

Field (1938) treated *philodice* and *eurytheme* as subspecies of *C. philodice*. It was his opinion that *C. philodice eurytheme* and *C. philodice eriphyle* were present in Kansas, and that *C. philodice philodice* was absent. He considered all yellow individuals in the area to be *C. philodice eriphyle*. Separation of *C. philodice philodice* and *C. philodice eriphyle* was based on the color of the central spot on the hind wing. The former had a straw colored central spot and in the latter this spot was orange. Clark (1941), discussing the genus *Colias* in North America, treated *philodice, eurytheme,* and *eriphyle* as intergrading forms of the European and Asiatic species *C. chrysotheme* Esper.

Hovanitz (1943, 1944, 1945) also considered *philodice, eurytheme,* and *eriphyle* as forms of *C. chrysotheme*. Gerould (1946), in a study of the hybridization of *philodice* and *eurytheme,* noted that the percentage of hybrids found in the field remained very low. He considered these two as species and felt that the use of *Colias chrysotheme* to cover *eurytheme* and *philodice* and their hybrids, was based on slight evidence, and was likely to confuse rather than promote taxonomy of the group. Hovanitz (1948, 1949, 1950), on evidence of other species of *Colias* hybridizing, returned to the binomial system and thus treats *philodice* and *eurytheme* as species. Remington (1954) and Dean (1956) likewise considered the two as separate species.

From the above review it can be seen that there is no generally accepted concept concerning the relationships in this complex. Because it best reflects the known situation and because it preserves the distinctness of the forms until more is known, *eurytheme, eriphyle,* and *philodice* will be considered as subspecies.

All material used in the following biological studies was collected in central California and hence involves only *eurytheme.*

Prior to 1900, *Colias philodice eurytheme* did not occur in the eastern United States. With the increase in acreage of alfalfa this form was able to move eastward (Hovanitz, 1944). Gerould (1946) reported approximately 9 per cent of the *Colias* population in New Hampshire to be *C. philodice eurytheme.*

Alfalfa (*Medicago sativa*) is the preferred host of *Colias philodice eurytheme,* and red clover (*Trifolium pratense*) is preferred by *C. philodice philodice.* According to Hovanitz (1948) *C. philodice philodice* does not find alfalfa a suitable host and *C. philodice eurytheme* does not find red clover suitable. White clover (*T. repens*) however, is a host common to both species and the preferred host of *C. philodice eriphyle.* This being the case, it seems probable that these *Colias* subspecies do remain separate, especially in areas where red clover and alfalfa are the most abundant hosts.

*Apanteles flaviconchae* does not seem to have any preferences between *Colias philodice eurytheme* and *C. philodice philodice.* Although it is generally associated with the latter, it has been recorded in *C. philodice eurytheme* on alfalfa (Floyd, 1940). Since in this case the parasites emerged from the fifth instar, which is never true of *A. medicaginis,* it seems certain that *A. flaviconchae* was involved. If it is true that *C. philodice philodice* is not found on alfalfa it is rather strong evidence that *A. flaviconchae* parasitizes both *C. philodice eurytheme* and *C. philodice philodice.* Unpublished data of the University of California Department of Biological Control show

that *A. flaviconchae* introduced from the eastern United States will successfully attack *C. philodice eurytheme* in the laboratory. Unfortunately, it is not known whether *A. medicaginis* will attack *C. philodice philodice.*

**Discussion.** On the basis of the above information it would seem that *Apanteles medicaginis* and *A. flaviconchae* developed to their present state of

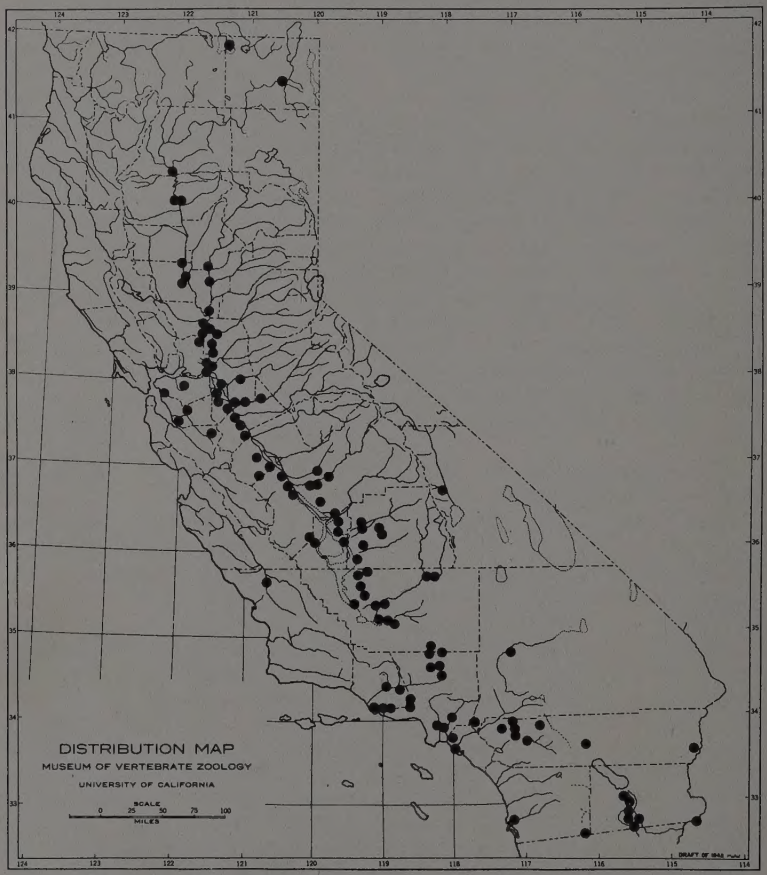



Fig. 1. The known distribution of *Apanteles medicaginis* in California.

distinctness while geographically isolated. With the increase in acreage of alfalfa and consequent spread of *Colias philodice eurytheme* to the eastern United States, it has been possible for *A. medicaginis* to extend its range beyond the Continental Divide. The two species, though still morphologically similar, are distinct in their biology. *A. flaviconchae,* at least, has not devel-

oped a host preference that distinguishes between *C. philodice philodice* and *C. philodice eurytheme*. During the same period the two *Colias* subspecies have developed differences in color, and to a slight degree in host preference, a tendency to prefer mating with their own kind, and other subtle biological characteristics.

Attempts to mate *Apanteles medicaginis* to *A. flaviconchae* in the laboratory resulted in male offspring, indicating that fertilization did not take place. Males of both species were attracted to females of the opposite species, but successful mating did not take place because the considerably larger size of *A. medicaginis* made copulation very difficult. When females were anesthetized with chloroform copulation did occur but in these limited trials fertilization did not take place.

It seems likely that these two species are at the present time reproductively isolated. If they were to occur in the same area, it is probable that *Apanteles medicaginis* would be intrinsically superior. Its internecine action (see p. 531) and earlier emergence from its host would probably preclude development of *A. flaviconchae* in a host parasitized by both species. However, actual superiority in any given area will be determined only when extensive studies are carried out on these two species.

Attempts to establish *Apanteles flaviconchae* in California by van den Bosch, Dietrick, and Hagen (1954) did not result in success. Although this might suggest superiority of *A. medicaginis,* it seems more likely that some other factor prevented successful establishment, for parasitism by *A. medicaginis* in the fields involved was not high.

## Distribution of *Apanteles Medicaginis* in California

Michelbacher and Smith (1943) showed that *Apanteles medicaginis* was distributed over many of the alfalfa growing areas of California. Since that time additional collections have been made, mostly on alfalfa, and a compilation of all these records is shown in figure 1. This does not mean that *A. medicaginis* is limited to these areas; it is merely a reflection of the higher populations of *Colias* on alfalfa and hence a greater probability that *A. medicaginis* will be collected. Parasitized *Colias* and cocoons of *Apanteles* have been collected in large numbers on *Sesbania macrocarpa* showing that this parasite is not restricted to *Colias* feeding on alfalfa. In addition, an *A. medicaginis* cocoon was collected on *Astragalus* sp. at a considerable distance from alfalfa, and another on *Lotus scoparius* (Nutt.) far from any alfalfa. It is probable that *A. medicaginis* is present in most areas of the western United States where *Colias philodice eurytheme* occurs on wild legumes.

*Apanteles medicaginis* has been collected most frequently in the central valleys of California but this again merely reflects the areas where *Colias* populations are highest. Coastal records are represented by the San Francisco Bay area, San Luis Obispo, Los Angeles, and San Diego. These valley and coastal records are all from low elevations, but others—Alturas, California (4,446 feet) and Minden, Nevada (4,750 feet)—are from considerably higher elevations.

The localities from which this species has been reported differ widely in temperature. Blythe, California, has a January mean temperature of 10.7°C

and a July mean of 32.8°; at the other extreme, Alturas has a January mean of –1.9° and a July mean of 19.3°. In between these two, the Dos Palos area (Los Banos) has a January mean of 8.9° and a July mean of 26.4°; and the San Francisco Bay area (Oakland) has a January mean of 8.4° and a July mean of 17.1°. Although maximum and minimum temperatures are more important than mean temperatures in the distributional limitation of insects, these mean temperatures suffice to show that *Apanteles medicaginis* has a wide temperature tolerance range.

In California, *Apanteles medicaginis* will probably be found in all areas where legume hosts are abundant enough to support a population of *Colias* sufficiently large for *Apanteles* females to find the individuals.

## Life History and Developmental Stages

Studies of the life history of a parasitic insect are generally more difficult than those of nonparasitic insects because it is necessary to develop satisfactory techniques for handling both the parasite and its host and to integrate them. In the case of *Apanteles medicaginis* and its host *Colias philodice eurytheme* this double problem was further complicated by the occurrence of a virulent virus disease in the *Colias* stocks (Steinhaus, 1948, 1949; Steinhaus and Thompson, 1949; Thompson and Steinhaus, 1950; Thompson, 1951). Special procedures had to be followed to prevent the spread of this disease. If aseptic methods were not followed or if several caterpillars were reared in a common container almost 100 per cent mortality resulted. The prevalence of this virus, *Borrelina campeoles* Steinhaus, necessitated sterilizing all equipment and rearing the *Colias* caterpillars individually.

**Rearing Procedures.** Eggs of *Colias* were obtained from field-collected adults because of difficulties encountered in obtaining mating of the butterflies in the laboratory. Intense sunlight and large numbers of adults confined in a cage would result in a few matings, but the proportion of females that mated was always low. This lack of mating and the complications of rearing made the use of field-collected females more practical except in the middle of winter when adults were not available in the field.

In the laboratory adult *Colias* were allowed to oviposit on cuttings of alfalfa or bur clover, the butterflies ovipositing readily when exposed to sunlight or intense artificial light. The eggs obtained were incubated on the cuttings. The incubation temperatures were varied to control the time of hatching, and thus the production of caterpillars was geared to the experimental needs. Thompson and Steinhaus (1950) developed a method for sterilizing eggs to inactivate the virus. In all experiments subsequent to their work the eggs were sterilized by placing them in 10 per cent formalin for 1 hour, which greatly reduced the amount of polyhedrosis.

Food for the caterpillars was provided by cutting off the terminal portion of alfalfa shoots. The stems of these cuttings were wrapped with cotton and placed in ½-dram vials filled with water. Sterile cotton and vials were used for this purpose, and the alfalfa had been grown in an area comparatively free of virus. Food vials were prepared only after thorough washing of the hands and when possible early in the day before the hands had become contaminated with virus. The prepared food vials were then placed in an

airtight container to prevent evaporation and contamination until they were to be used. Subsequent handling of the food vials was done with forceps sterilized by flaming.

In addition to alfalfa, *Medicago sativa,* both bur clover, *Medicago hispida,* and spotted medick, *Medicago arabica,* were used as food because of their availability in the winter. At Berkeley alfalfa dies back after the first cold weather, and at about the same time bur clover becomes abundant. All of these hosts were used extensively and there was no noticeable difference in their effect on *Colias philodice eurytheme* or *Apanteles medicaginis.*

Soon after the eggs hatched on the cuttings, the individual larvae were placed in separate petri dishes, which had been sterilized by boiling for 20 minutes. The larvae were transferred by means of a flamed needle to food prepared in the manner described above. Those larvae destined to be parasitized in the first instar were not transferred from the original leaflet until the time of parasitization, for even if some of these caterpillars were infected with the virus at the time of hatching they probably would not be able to infect the associated larvae during these first few days.

The food was changed at frequent intervals, depending on the size of the caterpillars and the temperature at which they were held. In all cases the food was changed when the leaves first showed signs of etiolating. The early-instar caterpillars were transferred from the old to the new food, for it was found that they would remain on the old food long after it had become unsuitable. After reaching the third instar, however, the caterpillars would crawl to the more suitable food and their transfer was no longer necessary.

Adult *Apanteles* were obtained by collecting cocoons and parasitized larvae in alfalfa fields and rearing the material through to the adult stage. The resulting adults were fed honey and raisins, and were kept in the dark when not actually being used to parasitize *Colias.*

Control of parasitization under aseptic conditions proved to be very difficult. The best method devised was slow and tedious but it minimized the chance of virus infection. The adult *Apanteles* that was to be used for parasitization was placed in a pint ice cream carton capped with a petri-dish top. A hole was cut in the side of the carton and a small cork inserted. A wire was forced into this cork, the free end of which was coiled so that an alfalfa leaflet could be placed on it. Leaflets bearing *Colias* larvae were placed on this wire coil with sterile forceps. The larva was then placed in the cage by inserting the cork in the hole in the carton. After being parasitized the caterpillar was removed and transferred with a flamed needle to new food.

This method had several advantages. First, the wire holder could be flamed after each larva was parasitized. Secondly, the leaf bearing the larva was held in position by the cork and did not require manipulation until parasitization had occurred. The need for such precautions against virus contamination was increased by the possibility that *Apanteles medicaginis* might be capable of transmitting *Borrelina campeoles* Steinhaus (Thompson and Steinhaus, 1950). This possibility is supported by the findings of Paillot (1924, 1926) and Chorine (1930), who recorded *Apanteles glomeratus* L. as a vector of a microsporidian disease of *Pieris brassicae* L.

Parasitized *Colias* caterpillars were held in the individual petri dishes until the *Apanteles* larvae emerged. Upon emergence, the *Apanteles* larvae spun cocoons on the leaves and the bottoms of the petri dishes. While the cocoons were present it was found necessary to keep a vial containing alfalfa cuttings in the petri dish to maintain favorable humidity conditions.



Fig. 2. Female *Apanteles medicaginis* Muesebeck (×28).

Most rearings were made at a temperature of 26.7°C (80°F) but studies on the rate of development were conducted at temperatures ranging from 15°C to 35°C. In all cases temperatures were controlled in cabinets provided with bimetallic thermostats and mercury relays. The cabinets were operated in rooms below the desired temperature so that only a heat source was necessary to maintain the proper temperatures. In all instances this heat source was provided by a light globe, the size depending on the differential between the room temperature and the desired temperature.

The light was always shielded in such a manner that neither the insects

nor the thermometer was directly subjected to radiant heat from the heat source. By such a method the ambient temperatures could easily be determined without undue complications from radiant heat.

Circulation of the air within the cabinets was maintained by an electric fan placed over the heat source. With this equipment and procedure the desired temperatures were maintained within 0.5°C.

**The Adult.** The adult of *Apanteles medicaginis* (fig. 2) was originally described by Muesebeck (1947) in the following manner:

*Female.* Length about 2.5 mm. Face smooth and shining; malar space at least one and one-half times as long as clypeus. Punctures of mesonotum very small but sharp and close throughout, in places confluent as noted above [i.e., on the posterior half of the mesoscutum, especially along the lines of the notaulices], scutellum convex with scattered weak punctures, shining; propodeum rugose with a complete median longitudinal carina and strong though incomplete costulae; mesopleuron closely punctate on lower half and anteriorly, smooth and polished above the longitudinal impression. Stigma barely twice as long as broad; radius strongly inclined outwardly, longer than intercubitus and joining it in a definite angle; nervellus strongly oblique but nearly straight. Calcaria of hind tibia subequal, slightly less than half as long as metatarsus.

Abdomen rather stout; plate of first tergite broadening apically, finely rugulose; second tergite nearly three times as long as broad, much shorter than third, closely rugulose with very narrow lateral polished margins; suturiform articulation sharply impressed minutely pitted; third tergite usually with a little indefinite sculpturing basally; hypopygium attaining apex of last tergite; ovipositor sheath barely exserted.

Black; maxillary palpae yellowish except toward base; labial palpae usually piceous, tegulae and radices black; stigma dark brown, most of the veins pale; legs reddish yellow with all coxae and trochanters, bases of fore and middle femora, apices of hind femora and hind tibiae, and the posterior tarsi, blackish.

*Male.* Like the female but with black hind femora.

The examination of large numbers of individuals in the current study has revealed considerable color variation. Some of this variation is undoubtedly an effect of temperature. Individuals subjected to low temperature during the pupal stage are much darker than those held at higher temperatures. Females reared under such conditions often have the posterior femora entirely black. Such an effect of temperature on insects have been widely reported (Knight, 1924; Genieys, 1925; Parker, 1930; Marcovitch and Stanley, 1930; Harries and Douglass, 1948; and others).

Size is another characteristic that varies considerably in the adult *Apanteles medicaginis,* as shown by the following data, based on measurement of 20 males and 20 females.

| | |
|---|---|
| Body, male | 2.0–3.0 mm, averaging 2.6 mm |
| Body, female | 2.4–3.5 mm, averaging 2.9 mm |
| Antenna, male | 2.7–3.4 mm, averaging 3.2 mm |
| Antenna, female | 2.4–2.8 mm, averaging 2.6 mm |

The measurements of body length were taken from the front of the head to the tip of the abdomen. Females average somewhat larger than males, but the variation within each sex overshadows the difference between the two sexes. The antennae of the males averaged 3.2 mm, which is considerably longer than the body length. The antennae of the females averaged 2.6 mm, somewhat shorter than the body length. This greater length of the

TABLE 2

DIFFERENTIAL EMERGENCE OF SEXES OF *APANTELES MEDICAGINIS* FROM *COLIAS* COLLECTED IN ALFALFA FIELDS NEAR DOS PALOS, CALIFORNIA

| Locality | Date | Total number of *Apanteles* and per cent females emerging on successive days | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | First | | Second | | Third | | Fourth | | Fifth | | Total emergence | |
| | | Total number | Per cent females | Total number | Per cent females | Total number | Per cent females | Total number | Per cent females | Total number | Per cent females | Total number | Per cent females |
| Oxalis A* | Aug. 24 | 36 | 33 | 96 | 65 | 27 | 78 | .. | .. | .. | .. | 159 | 60 |
| Oxalis B† | Aug. 24 | 9 | 55 | .. | .. | 40 | 28 | 62 | 52 | 13 | 69 | 124 | 46 |
| Oxalis B† | Sept. 7 | 19 | 32 | 65 | 32 | 99 | 24 | 120 | 44 | 81 | 69 | 384 | 39 |
| 7 miles N.W. Dos Palos* | Sept. 7 | 192 | 32 | 292 | 50 | 69 | 72 | 5 | 80 | .. | .. | 558 | 47 |

* Field-collected larvae.
† Field-collected cocoons.

male antennae results from the apical segments being much more elongate than those in the female. The apical segments of females are about as long as broad but those of males are about twice as long as broad.

After pupation the adult emerges from the cocoon by cutting a circular cap (operculum) out of the anterior end of the cocoon. When the adult has cut completely around the cocoon with its well-developed bifid mandibles, it forces itself out. The operculum is usually found pushed to one side, still attached by loose outer threads of silk. This characteristic operculum provides an accurate indicator of *Apanteles* emergence, for all known hyperparasites emerge through irregular holes, which can readily be distinguished from the operculum.

There was invariably a high percentage of males among the first parasites to emerge from field-collected cocoons or from cocoons spun by parasites emerging from field-collected caterpillars (table 2). Field sweeping of *Apanteles medicaginis* also revealed the earlier emergence of males; for when adults were gathered in fields in which the parasites were just starting to emerge, there was always a high percentage of males, whereas subsequent collection in the same field gave increasing proportions of females. The small difference in developmental time was not, however, evident in laboratory rearing.

The preoviposition period in this species, as with most *Apanteles,* is very short. Several hours after emergence the female is capable of oviposition, but the rate of oviposition and the stimulus to search for *Colias* increases for several days.

*Apanteles medicaginis,* when not mated, reproduces parthenogenetically. The progenies of unmated females are always males. This type of reproduction, which is common in most *Apanteles,* is covered in detail by Allen and Smith (1958) in their discussion on sex ratio.

Mating, which normally takes place soon after emergence, was not readily obtained in the laboratory. Males were attracted to females, but the females were reluctant to mate under cage conditions. Various methods were tried to bring about mating, but in all cases the number of successful matings was very low. The placing of starved females with food and well fed males proved to be of little value. Placing the adults in bright sunlight seemed to stimulate the sexual activity of the males but had little effect on the females. Increasing the chance of contact by placing large numbers of males and females in a cage seemed to be of some advantage, but the resultant number of mated females still remained low.

Males upon coming into close proximity with a female, manipulate their antennae and commence to flutter their wings. The female, if inclined to mate, spreads her wings, and then the male moves up onto the female from behind. The male then curves its abdomen down and inserts the aedeagus into the genital aperture of the female. Actual copulation requires a period of about 1 second.

*Apanteles medicaginis* lays a single egg within the body of small *Colias* larvae. The egg passes down the ovipositor, stalk first. Generally the eggs are found free in the haemolymph of the host, but on several occasions eggs were found attached by the short peduncle to internal structures such as

the gut, the silk glands, and the Malpighian tubules. These latter observations tend to substantiate those of Faure (1926), who found the eggs of *Apanteles glomeratus* attached to various internal structures.

Females searching for hosts are attracted by fecal pellets and by the "past presence" of a host larva in a certain area. The antennae are used constantly as the female searches. It would appear that sensory organs on the antennae are of primary importance in the search. Sight seems to be of little value. A host larva may be nearby, but if the antennae of the female do not come in contact with the larva the female continues searching. Upon coming into contact with a suitable host the female immediately jumps upon the caterpillar and inserts her ovipositor in one swift motion. The act of oviposition requires about 1 second, and even though the host reacts violently, the ovipositor usually remains inserted for the required length of time.

*Apanteles medicaginis* will oviposit in first-, second-, and third-instar host larvae, but field observations suggest that the first instar is preferred. Eggs laid in the early first-instar larva result in emergence from the third instar, whereas eggs laid in the late first, second, and third instar result in emergence from the fourth instar. From this it might be expected that the majority of individuals would emerge from the fourth instar, but this does not seem to be true. Field observations made during the course of this work indicate that the majority of the individuals emerge from the third rather than the fourth instar. Since this held true even in fields in which the percentage parasitization was not excessively high, and hence second- and third-instar *Colias* were available for attack, it strongly suggests that *A. medicaginis* prefers to oviposit in very small *Colias* larvae.

*Apanteles flaviconchae* has been found to occur in nature on the following hosts: *Colias philodice philodice* Godart, *Anthocaris genutia* Fabr., *Plathypena scabra* and *Pseudalctia unipuncta* (Haw.) (Muesebeck 1921). *A. medicaginis* on the contrary has only been found to parasitize *C. philodice eurytheme*. Numerous lepidopterous larvae have been reared from alfalfa fields that contained large numbers of *A. medicaginis* adults, but this parasite was never reared from any other host than *C. philodice eurytheme*. In the laboratory *A. medicaginis* females were confined with larvae of *Pieris rapae* and *P. protodice* but the *Apanteles* were not stimulated to oviposit. Even when the *Pieris* larvae were placed on alfalfa leaves there was still no oviposition by *Apanteles*.

**The Egg.** Immediately after deposition the *Apanteles medicaginis* egg (fig. 3,A) is cylindrical, slightly curved, with rounded ends. At the caudal end it bears a short, slightly curved peduncle. The chorion is thin, transparent, and devoid of surface sculpturing. At this time the egg averages about 280 microns in length and 61 microns in width, and the peduncle measures about 24 microns.

The egg, which is generally found free in the body cavity of the host caterpillar, may be found anywhere in the body except in the head capsule. Immediately after deposition the embryo begins to increase in size. The increase is more pronounced in the transverse direction, so that immediately prior to hatching, the egg (fig. 3,B) has a robust appearance, averag-

ing about 443 microns in length and 176 microns in width. A similar increase in the size of the eggs has been reported for *Apanteles thompsoni* (Lyle) (Vance, 1931), and in certain Euphorinae and Meteorinae the increase is even greater (Ogloblin, 1913; Balduf, 1926; and Strickland, 1923). The embryo developing within the egg is clearly visible through the transparent chorion. It is situated in the center of the egg and is completely surrounded by the cells of the serosa (Tower, 1915; Vance, 1931).

After an incubation period of 24 to 30 hours at 26.7°C, the larva emerges. The larva curves its body so that the mandibles are forced against the elastic side of the egg and manipulates the mandibles in a transverse direction until the egg bursts. Upon rupture of the chorion, the larva and the numerous cells of the serosa burst out into the blood of the host. For a considerable time after hatching these cells can be found attached to the larva.

**First-Stage Larva.** The newly hatched larva (fig. 3,C) is about 472 microns long, with the head, the widest part, being about 161 microns wide. It is translucent and distinctly segmented. The head, which is rather square with distinct mandibles, and the caudal horn are the prominent structures of this stage. The body is made up of three thoracic and seven abdominal segments, which, except for the first thoracic segments, bear a single transverse row of sharp, translucent dorsal spines. The number of spines on any one segment is variable, but increases posteriorly.

Like the egg, the newly hatched larva can be found in almost any part of the caterpillar. By the time the first-stage larva is ready to molt, however, it has oriented itself, head forward, in the posterior portion of the host, where it remains until emergence. The first-stage larva is the same as the first instar.

During the first larval stage the well-developed mandibles are constantly in motion. It is through use of these mandibles that any other *Apanteles* larvae encountered in the same host are destroyed. Gregarious species, such as *A. flaviconchae,* do not exhibit this internecine action, and in some, such as *Apanteles ruficrus* Hal., the first-instar larvae are completely enveloped in a trophamnion (Hafez, 1947).

At the time of hatching an anal vesicle is not visible, but as the larva grows this structure becomes evident and by the time of the first molt it has become quite prominent. During this same period the head and caudal horn become relatively inconspicuous. Just before the first molt the larva is about 1.4 mm long, having tripled in length from the time of hatching.

The time required for development through the first molt varied greatly according to the size of the host caterpillar. At 26.7°C this period varied from 3.5 days to 5.5 days, the longer period being required by those in very small host caterpillars. Since hatching of the egg requires about one day, the time spent in the first instar ranges from 2.5 to 4.5 days.

**Second-Stage Larva.** The second-stage larva (fig. 3,D) differs greatly from the preceding stage. The head is no longer sclerotized and the mouthparts are poorly developed, the mandibles being composed of fleshy lobes. The body is distinctly segmented; there are now eight instead of seven abdominal segments and the abdominal spines are lacking. The body is more opaque because of the developing silk glands. The anal vesicle is greatly

enlarged, becoming a very prominent structure, while the caudal horn is quite inconspicuous.

During the second stage the larva enlarges from a length of about 1.4 mm at the start to about 6.9 mm just before molting to the third stage. This very great enlargement suggests the possibility that the second stage is

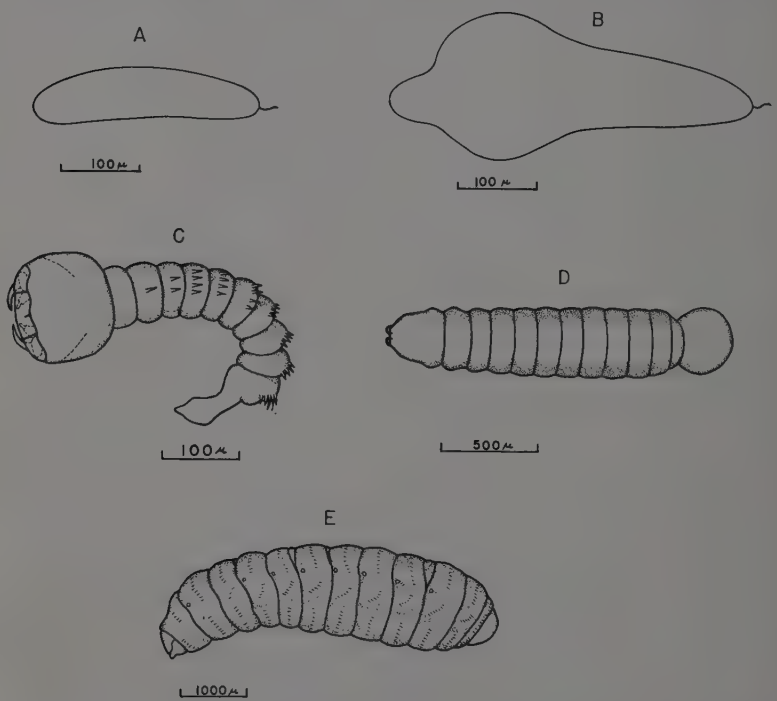



Fig. 3. Egg and larval stages of *Apanteles medicaginis* Muesebeck: *A*, newly laid egg; *B*, egg just prior to hatching; *C*, first-stage larva; *D*, second-stage larva; *E*, third-stage larva.

made up of two instars. However, the complete absence of sclerotized structures makes it very difficult to determine the occurrence of another molt during this stage. Although numerous workers have studied various species of *Apanteles*, it has never been clearly demonstrated that there is an additional instar (Grandori, 1911; Parker, 1935; De Saeger, 1942). Careful study of the development of the second-stage larva of *Apanteles medicaginis* does not reveal any indication of an extra instar. In such an amorphous form the great increase in size probably does not require a molt. Such increase is not uncommon in other parasitic Hymenoptera (Clausen, 1940) and has been reported for the parasitic beetle *Rhipiphorus smithi* (Linsley, MacSwain, and Smith, 1952). The terminology of the first-stage, second-

stage, and third-stage larva, should be retained because of the marked differences in morphology and the possibility that the second-stage larva represents two or more instars.

The molt at the completion of the second stage does not take place until just before emergence of the larva from the host. Although the characters of the third-stage larva are clearly visible some time before emergence begins, the integument of the second-stage larva envelops the larva until emergence. In order to tear its way out of the host, the larva must molt; but it is evident that the molt takes place at this time and not earlier, for the cast skin is always found exactly at the point of emergence. This habit allows the third-stage larvae, which has exposed spiracles, to survive inside the host. This adaptation is characteristic of most Microgasterinae but an exception occurs in *Apanteles lacteicolor* Vier. (Clausen, 1940). The delayed molting of the second-stage larva also creates a problem as to the exact point of completion of this stage. Is the second stage completed when the characters of the third stage become visible through the integument, or is the second stage completed when the skin is cast?

At 26.7°C the total time spent in the *Colias* larva varied from 7.5 to 10 days depending on the size of the caterpillar when parasitized. Assuming the second stage is completed when the skin is molted and allowing 3.5 to 5.5 days for the egg and first-stage larva, it can be estimated that the second-stage larva requires 4.0 to 4.5 days to complete its development.

Numerous workers state that *Apanteles* larvae feed directly on the fat body and vital organs of the caterpillar (Gatenby, 1919; Vance, 1931; De Saeger, 1942), but this does not seem to be the case with *A. medicaginis*. It is only during the first and last instar that this could take place, for the second instar has very poorly developed mandibles. Prior to emergence of the *Apanteles* the caterpillar stops feeding, often moves upward on its host plant and spins a small silken mat beneath itself. Here it remains until the parasite emerges. Since it is not until the parasite has reached the second stage that the host caterpillar shows any external reaction to parasitism and since the parasite molts to the third instar just prior to emergence, it does not seem probable that *A. medicaginis* feeds to any extent on the fat body or the vital organs. It is more plausible that devitalization of the caterpillar results from starvation induced by the parasite's utilizing most of the food assimilated by the caterpillar.

**Third-Stage Larva.** The third-stage larva (fig. 3,E) tapers anteriorly and is more robust than the earlier stages. At this time the larva is about 4.5 mm long. The anal vesicle, quite large at the end of the second stage, is no longer present. The larva is creamy white in color and very opaque because of the greatly enlarged silk glands. The head is small with well-developed mouth parts. The mandibles are heavily chitinized and bear many sawlike teeth, which the larva uses for tearing its way out of the host. Segmentation of the body is distinct; there are now three thoracic and ten abdominal segments. Each segment bears numerous small spines. Prior to this stage, spiracles have been absent, but in this stage there are spiracles on the mesothoracic and first seven abdominal segments.

Immediately after molting to the last instar, the larva begins to emerge from the host caterpillar. The instar of the host at this stage is dependent

on the time at which it was parasitized. As was pointed out by Michelbacher and Smith (1943), oviposition by the parasite in the first instar results in emergence from the third instar, whereas oviposition in the second or the third instar results in emergence from the fourth instar. However, data gathered by the author indicate that parasitization in the late first instar often results in emergence from the fourth instar.



Fig. 4. Above, larva of *Colias philodice eurytheme* showing emergence hole of *Apanteles medicaginis*. Below, freshly spun cocoon of *A. medicaginis*.

When the larva is ready to pupate, it cuts its way out of the caterpillar. External observations indicate that this is done by the larva's forcing its head against the side of the host caterpillar, and moving back and forth in a longitudinal direction. It would appear that the mandibles are used in a rasping manner. The place of emergence is usually along the lateral line of the caterpillar (fig. 4), the exact position being determined by the relative size of the host and the parasite larva. As internal tissues are ruptured, a distinct bulge is formed, and the caterpillar takes on a characteristic crooked form due to the pressure exerted by the parasite within. After

about 5 minutes the outer wall ruptures and the parasite head becomes visible. At this time the parasite often becomes quiescent for about 1 minute and then proceeds to emerge. This is done by a peristaltic action of the larva. When the larva is about two thirds out of the host it begins to spin its cocoon. This partial spinning before complete emergence is an important characteristic, for often the host caterpillar clings to a ventral surface and the parasite would fall to the ground if it emerged completely before spinning part of the cocoon.

At first the parasite spins the loose outer filaments which attach the cocoon to the substrate. In constructing the original framework of the cocoon the parasite utilizes both the caterpillar and its own body for temporary attachment of the silk. After this rough framework has been established, the larva completes its emergence from the caterpillar. Soon after complete emergence the parasite reverses its position and forces the caterpillar away with its head. Because of this pushing action, host caterpillars are seldom found associated with cocoons. By this time the caterpillar is in a moribund condition, and although actual death may not result for some time, the caterpillar is incapable of feeding or locomotion. The caterpillars do not survive for long periods of time as has been reported for some individuals of *Pieris* attacked by *A. glomeratus* (Gatenby, 1919), and *A. rubecula* Marsh (Blunck, 1951). The parasite after completion of the loosely woven outer envelope constructs a finely woven inner silken lining. Several hours are required for completion of the cocoon and during the course of construction the larva reverses its position repeatedly.

The completed cocoon (fig. 5) is oblong with rounded ends. At the point of attachment to the substrate it is somewhat flattened and the silken wall is considerably thinner. Measurement of 20 cocoons gave an average length of 4.3 mm and an average width of 1.9 mm.

Cocoons are normally yellow but occasionally may be very pale yellow or white. This white color in the case of *Apanteles flaviconchae* was explained by Gerould (1921) on the basis of the pigments available in host larvae. He found that *A. flaviconchae* cocoons from normal yellow-green caterpillars of *Colias philodice* were yellow but cocoons spun by larvae emerging from blue-green caterpillars were white. This has not been substantiated for *A. medicaginis,* but it is probably the explanation for white cocoons in both species.

Disposition of the cocoons is determined by the location of host caterpillars at the time of parasite emergence. Since parasitized caterpillars tend to crawl upward before emergence of the parasite, cocoons are often found on the upper leaves of alfalfa plants. They can be found lower down, however, sometimes on the stems of alfalfa plants and occasionally on plants that are not hosts of *Colias.* These latter probably represent instances where parasitized caterpillars have fallen to the ground a short time before emergence of the parasite and have crawled up the nearest available vegetation.

**The Pupa.** About 24 hours after emergence from the host, the parasite voids its dark green meconium, and a short time later pupation takes place. At first the pupa is light yellowish, but as it matures it becomes increasingly darker so that just before adult emergence it is nearly black. As is true of most Hymenoptera, the pupa has the general appearance of the adult, and

the appendages, although not movable, are clearly visible. At 26.7°C the time spent in the cocoon is approximately 4.5 days, about 3 days of which are passed in the pupal stage.

## Seasonal History of *Apanteles Medicaginis*

Members of the genus *Apanteles* vary greatly in their seasonal history and biology (Clausen, 1940). There are usually several generations each year and the generations are relatively short. Most of the species pass the winter



Fig. 5. Cocoons of *Apanteles medicaginis* Muesebeck showing operculum.

as first-instar larvae in their hosts, although *A. glomeratus* and *A. solitarius* may at times occur in winter as mature larvae in the cocoons. A considerable variation is shown in the position taken by the larvae at the time of cocooning. Much of this variation is explained by the differences in seasonal history of the hosts. For example, immature larvae of a species can only overwinter when host caterpillars are present throughout the winter, and the number of generations per year is closely correlated with the length of time host caterpillars are available.

Periodic sweeping of alfalfa in the San Joaquin Valley indicates that *Apanteles medicaginis* overwinters in the larval stage as was shown to be true for *Colias philodice eurytheme* in the same area (Smith, Bryan, and Allen, 1949). Although populations of *Colias* are low during the winter,

there are always some parasitized caterpillars present. The majority of the overwintering caterpillars, both parasitized and nonparasitized, in any one area are usually found in a very small number of fields. This concentration of the overwintering population in a few fields is dependent upon the overwintering condition of the alfalfa and the population present at the time subdevelopmental temperatures set in. Since the overwintering population stems from the fall generation, when populations of both host and parasite are comparatively high, the proportion of caterpillars parasitized is likewise high.

Adult *Apanteles* have been collected throughout the year, but their numbers are always low during the winter months. Since adults proved to be rather delicate and very dependent on food in the laboratory, it does not seem likely that this species can survive through the winter as an adult. The few adults encountered probably represent individuals which emerged from overwintering cocoons. Since cocoons have not been found during the winter, they probably represent a very small portion of the overwintering *Apanteles medicaginis* population; however, it must be kept in mind that cocoons cannot be swept from alfalfa like adults and parasitized larvae, and hence are much more difficult to detect. It is also quite possible that some cocoons occur in the litter, where they would be very difficult to detect. Parasitized caterpillars have been collected throughout the winter, and although cocoons have been collected late in the fall, there has been no indication of a diapause in *A. medicaginis*. Furthermore all stages have been subjected to low temperatures in the laboratory, and in every case development recommenced when the temperature was increased. Since cocoons have never been collected during the winter and there is no true diapause in *A. medicaginis*, it does not seem likely that the cocoon plays an important role in overwintering. Thus it can be concluded that *A. medicaginis* overwinters primarily as immature larvae inside the caterpillars. Development is merely arrested during the winter and with the advent of warm weather it recommences. The number of generations each year is dependent on the climate of the area and the availability of host caterpillars. (For further details on the seasonal history of *A. medicaginis* and *Colias philodice eurytheme*, see Allen and Smith, 1958.)

## SUMMARY

The alfalfa caterpillar, *Colias philodice eurytheme* Boisduval, is an important pest of alfalfa in California. *Apanteles medicaginis* Muesebeck is the most prevalent parasite of the alfalfa caterpillar and is an important factor in its control. This species is a solitary internal parasite. It is distributed over much of California and has also been found in Arizona, Idaho, Nevada and Kansas. In the eastern United States a closely related species, *A. flaviconchae* Riley, has been recorded from both *Colias philodice philodice* Godart and *Colias philodice eurytheme* Boisduval. *A. flaviconchae* is a gregarious parasite and biologically distinct from *A. medicaginis*.

*Apanteles medicaginis* oviposits inside first-, second-, and third-instar host caterpillars. The egg, which is generally found free in the body cavity, begins to develop immediately after deposition and as development continues it increases strikingly in size. The first-stage larva is very active, with highly

functional mandibles, whereas the second-stage larva is quiescent, with the mandibles reduced to fleshy lobes. This second-stage larva, which may be comprised of one or two instars, molts a final time just as it emerges from the host caterpillar. The wound inflicted by parasite emergence causes rapid death of the host. The third-stage larva begins to spin its small, yellow cocoon before emergence from the host caterpillar is completed. Pupation takes place wherever the host caterpillar happens to be at the time the parasite emerges.

*Apanteles medicaginis*, which shows no evidence of a diapause, overwinters as a larva inside the host caterpillar. Populations are relatively low during the spring because of low host density, but after a number of generations the parasite often becomes abundant on the relatively high *Colias* populations which develop in the summer and autumn.

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